A STUDY ON THE VARIABILITY OF THE SKELETON OF *LATES NILOTICUS* (LINNAEUS, 1758) IN VIEW OF THE VALIDITY OF *LATES MALIENSIS* GAYET, 1983

by

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ABSTRACT. - The validity of *Lates maliensis* Gayet, 1983, described from Holocene deposits of the Malian Sahara, is disputed. The majority of the features that characterize *L. maliensis* were also observed in a sample of 18 recent *L. niloticus* specimens from the Nile and Niger basins. Some characteristics of *L. maliensis* seem to hold, but closer examination of these features demonstrates that partial destruction of certain *L. niloticus* bony elements can give them a *L. maliensis* appearance. Therefore *L. maliensis* Gayet, 1983 is considered to be a synonym of *L. niloticus* (Linnaeus, 1758).

RESUME - Etude de la variabilité du squelette de *Lates niloticus* (Linnaeus, 1758) en vue de la validité de *Lates maliensis* Gayet, 1983.
La validité de l'espèce *Lates maliensis* Gayet, 1983, décrite des dépots holocènes du Sahara malien, est discutée. La plupart des caractères morphologiques qui seraient typiques de *L. maliensis* ont également été observés dans un échantillon de 18 squelettes récents de *L. niloticus* provenant du Nil et du Niger. Certains caractères de *L. maliensis* sont valables à première vue, mais un examen plus profond indique que la destruction partielle de minces parties osseuses de certains os de *L. niloticus* peut leur donner une apparence de *L. maliensis*. Pour ces raisons *L. maliensis* Gayet, 1983 est considéré comme synonyme de *L. niloticus* (Linnaeus, 1758).

Key words: Centropomidae, *Lates niloticus*, *Lates maliensis*, Mali, Palaeontology, Osteology, Taxonomy.

In a part of the Malian Sahara (19-22°N/5-1°W), fieldwork has been carried out under the direction of Prof. N. Petit-Maire in 1980 and 1981. The results of this first series of campaigns have been brought together in an interdisciplinary monograph (Petit-Maire and Riser, 1983). Upper Quaternary deposits of the Taoudenni Basin were investigated from geological, geomorphological, palaeobotanical, palaeozoological, palaeoanthropological and archaeological points of view. The investigated area was characterized during the Holocene by an important lacustrine phase between some 9500 and 4500 B.P., interrupted by a minor arid oscillation from 6500 to 5500 B.P. Some lakes, which were fed by precipitation and by an aquifer rise, must have reached a surface of approximately 500 km2 and a depth of 15 m. Faunal and floral remains were abundant in the Holocene deposits and indicate a complete subtropical trophic chain. The species must have migrated after the preceding arid phase around 15000-18000 B.P. Whereas migration of mammals, reptiles and aquatic invertebrates do not necessarily imply the existence of permanent waterbodies, the presence of certain fish needing perennial waters are of great value for palaeohydrographic interpretations. According to Gayet (1983) the

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ichthyofauna consists of several taxa, but an exact quantification of their relative abundance is impossible since the number of specimens is only occasionally given. The majority of the remains belong to a new species *Lates maliensis* Gayet, 1983, but an appreciable number of clariids have been found as well. These catfish bones were identified by Gayet (*ibid.*) as *Heterobranchus* cf. *longifillis*, although the figured pectoral spine (Pl. XVII-2) clearly belongs to the genus *Clarias* according to the criteria established by von den Driesch (1983). Other siluroids found in the Holocene deposits are *Chrysichthys* sp., *Arius* sp. and *Synodontis* sp. Small quantities of the characid *Alestes* and of the cichlid taxa Tilapiinae and Haplochrominae were recovered as well. The presence of large *Lates* (more than one meter) indicates that permanent, deep and well-aerated water must have existed near the sites.

Important palaeohydrographic implications result from these findings. Since *Lates* lived in the lakes of the Hassi-el-Abiod area (± 19°N 4°W) a connection is supposed with the Niger river, situated today some 300 km more southward.

Moreover, the presence during the Holocene of fish with high ecological requirements (perennial, deep and well oxygenated water) in the region of Tagnout-Chaggaret (21°30'N 1°W) indicate that the Tilemsi river was running in a north-south direction and that active tributaries were present, allowing Niger fish to colonize an area which is situated at some 300 km west of the Tilemsi valley. A third palaeohydrographic result from the ichthyofaunal study is the supposition that a connection must have existed between the Senegal and Niger basin at a period not yet precisely dated.

The *Lates* bones from the Holocene deposits in Mali have been compared osteologically by Gayet (*ibid.*) with recent *L. niloticus* and *L. calcarifer*. The latter species is the only marine form of the genus, living today in coastal waters of the Indo-Pacific region. According to Gayet (*ibid.*), it is impossible to identify the *Lates* remains from Mali as *L. niloticus*, and on the contrary they display more affinities with *L. calcarifer*. A marine, or estuarine *Lates* sp. is known from the Miocene of Lissabon (Sorbini, 1973). Gayet (*ibid.*) supposes that this form, or an ancestor of it, has migrated along the Portuguese and African coasts as far as the Senegal river mouth. From there the formerly connected Senegal as well as the Niger river basins were colonized. A colonization of the Niger river from the sea was not possible since a connection with the Gulf of Guinea was formed until very recent geological times.

A second, though less likely (Gayet, *ibid.*, p. 195), route has been described for *L. maliensis*. The Nile, Tchad and Niger basins would have been connected during pluvial phases of the Plio-Pleistocene period allowing *L. niloticus*, known since the Pliocene from the Nile, to colonize West African waters. *Lates maliensis* would have existed sympatrically with *L. niloticus* and would have followed the same route. Gayet (*ibid.*) reckons it would be worth revising all the other reported remains of Holocene *L. niloticus* in order to check if some may represent *L. maliensis*.

Before detailing the palaeozoogeography, it is necessary to verify the validity of *L. maliensis*, which is described on the basis of isolated skeletal elements. In this study the variability of recent *L. niloticus* skeletons from the Nile and Niger is considered and the implications for recognizing *L. maliensis* are given.

MATERIAL AND METHODS

The figures and descriptions of *L. maliensis* were compared with 18 disarticulated skeletons of recent *Lates niloticus* (see Table I). This material was prepared during three missions in Egypt and one campaign in Niger and, together with skeletons of a large number of other species, serves as a reference collection

Table I. List of recent *Lates niloticus* skeletons used in the present comparative osteological study.

Specimen number	Locality	Approximate date of capture	Standard length (SL) (cm)	Total length (TL) (cm)	Fresh live weight (g)	Basal length of skull (BL) (mm)
286	market Niamey, Niger	05.05.86	27	31.5	350	65.0
278	"	03.05.86	31	36.5	550	78.0
227	"	23.04.86	33	38	740	78.5
302	"	06.05.86	35	41	800	81.6
301	"	06.05.86	36	42	950	84.2
312	"	14.05.86	38	44	1100	90.5
267	"	30.04.86	70	82	-	172.0
240	"	30.04.86	75	85	-	167.5
275	"	02.05.86	79	90	-	192.3
276	"	02.05.86	80	91	-	193.0
24	High Dam Lake, Egypt	Sept. 83	13	16	20	34.1
22	"	Sept. 83	15	22	100	46.0
67	"	Febr. 84	± 20	-	-	51.5
20	"	Sept. 83	26	32	400	69.1
81	"	Febr. 84	30	35	450	70.7
1	"	Sept. 84	46	53	1900	115.2
57	"	Sept. 83	52	51	2600	133.5
140	"	Nov. 85	110	125	-	262.5

for the identification of fish remains found in African archaeological sites (Van Neer, 1984).

The variability in *L. niloticus* has been examined for each character described by Gayet (1983) as being diagnostic for *L. maliensis*. Wherever possible morphological differences are expressed with the aid of measurements, in order to quantify certain statements in the literature (Fig. 1). Bone measurements were taken with a slide gauge.

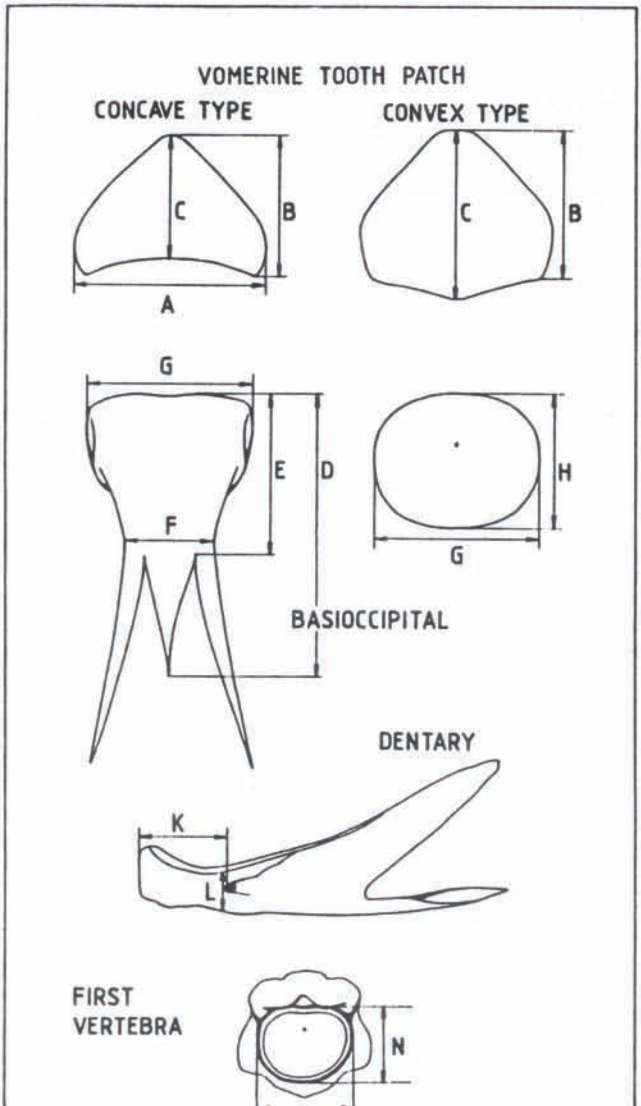


Fig. 1 : Measurement taken on various skeletal elements of *L. niloticus*.

RESULTS

VOMER

According to Gayet (1983, p. 187 and Fig. 33) the shape of the vomerine tooth patch is different in *L. maliensis* and *L. niloticus*. In *L. maliensis* the posterior edge is always convex, whereas it is said to be more or less concave in the other species. Judging from the recent *L. niloticus* specimens at our disposal, however, the shape of the tooth patch is extremely variable (Fig. 2). The most common type is indeed the one with a concave posterior margin (10 specimens out of 18). A rather straight border was observed in three specimens, whereas in only one the typical shape of *L. maliensis* was found. In the other four recent *L. niloticus* specimens, yet another shape was seen: the tooth patch terminates posteriorly as a low peak, extending beyond the line connecting the two lateral tips.

An attempt has been made to quantify the differences in outline by taking measurements on the tooth patches (Table II). From these data it is clear that the variation in shape is not correlated with age. Similar observations have been made for *Lates rhachirhinchus* from Neogene sites in northeastern Zaïre (Greenwood and Howes, 1975, p. 84).

The convex type of vomerine tooth patch thus seems to be rather rare among modern *Lates niloticus*, but it is possible that in fossil assemblages the ratio is higher as a result of partial destruction ot the bone. In a small sample of Holocene remains from an archaeological site in the Azawak valley in Niger (excavations by F. Paris, Niamey), we found one *Lates* vomer from an individual of approximately 1 meter standard length. The lateral edges and part of the posterior margin of the tooth patch were crumbled away, giving a convex outline to a specimen that originally must have had a rather straight or slightly concave posterior border.

LATERAL ETHMOID

The posterior margin of the lateral ethmoid is almost vertically aligned in both *L. niloticus* and *L. maliensis*, but there is reported to be a difference in width.

fig. 2

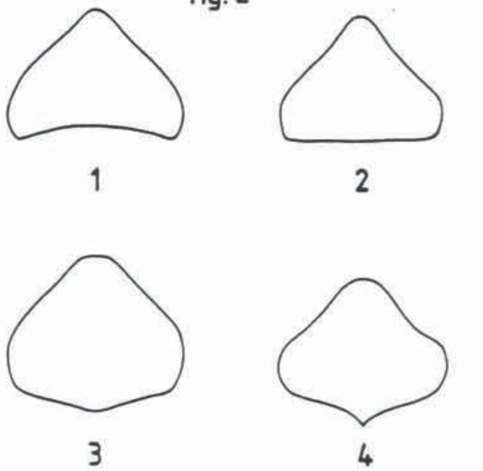


Fig. 2 : Types of vomerine tooth patch observed on recent *L. niloticus* specimens from the Nile and the Niger. 1: concave type; 2: straight type; 3: convex type; 4: pointed type.

Table II. Measurements taken on the vomer of recent *L. niloticus* specimens from the Niger and Nile.

	Nr	SL (cm)	A (mm)	B (mm)	C (mm)	C / B	Tooth patch type
Niger	286	27	7.0	5.1	3.9	.87	concave
	278	31	7.9	5.8	4.5	.78	concave
	227	33	8.6	5.5	5.3	.96	concave
	302	35	9.1	6.3	5.8	.92	concave
	301	36	8.0	6.4	6.2	.97	straight
	312	38	9.9	7.8	6.5	.83	concave
	267	70	17.1	13.3	14.7	1.11	convex
	240	75	17.6	13.3	12.4	.93	concave
	275	79	20.3	14.6	13.3	.91	concave
	276	80	20.3	14.9	12.6	.85	concave
Nile	24	13	3.5	2.5	1.9	.76	concave
	22	26	4.6	3.3	3.5	1.06	pointed
	67	± 20	4.8	3.1	3.2	1.03	pointed
	20	26	7.4	4.8	4.8	1.00	straight
	81	30	7.2	5.5	4.8	.87	concave
	1	46	12.0	9.4	9.8	1.04	pointed
	57	52	13.2	10.5	10.2	.97	straight
	140	110	30.2	22.0	24.5	1.11	pointed

In dorso-anterior view the lateral ethmoid of *L. niloticus* is said to be narrower than in *L. maliensis*. We were unable to evaluate this criterion with the aid of the figured isolated specimen of *L. maliensis* (Gayet, 1983, Pl. XVI-7), since the angle at which the lateral ethmoid is viewed, determines to a great extent its general appearance.

L. niloticus is, moreover, reported to differ from *L. maliensis* in its larger olfactory nerve foramen that is directed more anteriorly. In our sample of recent *L. niloticus* skeletons, we noticed an important variation in size, shape and direction of the olfactory foramen, leading us to the conclusion that this feature must be of restricted diagnostic value.

PARASPHENOID AND BASIOCCIPITAL

Gayet (1983, p. 187) describes four distinguishing features for the parasphenoid-basioccipital region, none of which seem to be valid. The parasphenoid becomes bifid in the contact zone with the basioccipital, and differences are said to exist in this area between *L. niloticus* and *L. maliensis* (Gayet, 1983, Fig. 34). In *L. maliensis* the two posterior forks of the parasphenoid are long, whereas in *L. niloticus* they are reported to be short and more widely separated. Of our entire sample of 18 recent skeletons, only one individual (nr. 276) resembled the figured *L. niloticus* specimen. All the other skulls showed "long" to "very long" forks contacting the basioccipital. In order to quantify this feature the ratio was calculated of measurements E and D (see Table III).

At the ventral side of the basioccipital there is a median cavity which in *L. maliensis* never extends as far as the parasphenoid. According to Gayet (1983), however, in *L. niloticus* the median cavity meets the parasphenoid. I observed a wide variation in length of the median cavity in the recent *L. niloticus* skulls, but in not

Table III. Measurements taken on the parasphenoid and basioccipital of recent *L. niloticus*

	Nr	SL (cm)	D (mm)	E (mm)	D/E	F (mm)	G (mm)	F/G	H (mm)
Niger	286	27	9.6	3.9	0.41	3.6	5.2	0.69	4.7
	278	31	9.6	5.0	0.52	3.7	6.2	0.60	6.0
	227	33	10.1	5.4	0.53	3.5	7.0	0.50	6.4
	302	35	12.4	6.4	0.52	4.8	7.1	0.68	6.6
	301	36	11.0	6.2	0.56	4.8	7.3	0.66	6.7
	312	38	12.6	6.7	0.53	5.0	8.1	0.56	7.3
	267	70	26.5	13.6	0.51	9.2	16.4	0.56	14.5
	240	75	22.8	13.1	0.57	9.6	15.7	0.61	13.8
	275	79	28.6	15.5	0.54	9.3	18.4	0.51	16.4
	276	80	24.0	16.1	0.67	11.3	18.6	0.61	16.2
Nile	24	13	5.1	2.1	0.41	1.4	2.4	0.58	2.1
	22	18	7.6	2.0	0.26	1.9	3.4	0.56	3.2
	67	± 20	-	-	-	2.1	3.5	0.60	3.3
	20	26	9.8	4.6	0.47	3.2	5.7	0.56	5.0
	81	30	10.0	5.5	0.55	3.4	6.2	0.55	5.4
	1	46	16.5	9.4	0.57	5.6	10.7	0.52	9.4
	57	52	19.9	10.7	0.54	7.3	12.1	0.60	10.2
	140	110	37.6	22.7	0.60	17.2	27.5	0.63	26.2

a single specimen does it extend as far posteriorly as to contact with the parasphenoid.

Two lateral facets are observed on the basioccipital of *Lates*. According to Gayet (*ibid.*) the position of the facets is of value in discriminating *L. niloticus* and *L. maliensis*. In the former species they are always clearly visible when the skull is ventrally viewed, whereas in *L. maliensis* they are hardly visible from that position. The attempted verification of this character - one that is again difficult to quantify objectively - has revealed much variation. The facets are clearly or partially visible in most examined recent *L. niloticus*, but in two specimens they are invisible in ventral view.

A fourth difference is said to lie in the shape of the posterior part of the basioccipital. According to Gayet (*ibid.*), when viewed posteriorly the basioccipital of *L. maliensis* is wider than high, whereas in *L. niloticus* it is always higher than wide. As can be seen from our Table III (measurements G and H), the basioccipital is always wider than high in *L. niloticus*, as it is the case for *L. maliensis*.

Gayet (*ibid.*) also mentions that in *L. niloticus* the posterior part of the basioccipital generally widens, at least in large individuals. In *L. maliensis* a posterior widening may sometimes occur. For the sake of completeness the degree of enlargement was quantified by calculating the ratio of the smallest width of the basioccipital - parasphenoid region and the greatest breadth of the basioccipital articular surface (measurements F and G in Table III). Some variability is observed but seems not to be correlated with size.

Table IV. Degree of development of the groove in the exoccipital leading to the foramen for the vagus nerve in recent *L. niloticus*.

	Nr	**SL (cm)**	**Well developed groove**	**Poorly developed groove**	**no groove**
Niger	286	27			*
	278	31			*
	227	33			*
	302	35			*
	301	36			*
	312	38			*
	267	70	*		
	240	75		*	
	275	79	*		
	276	80	*		
Nile	24	13			*
	22	18			*
	67	± 20			*
	20	26		*	
	81	30			*
	1	46	*		
	57	52		*	
	140	110	*		

PROOTIC

The prootic of *L. maliensis* would appear to differ little from other species (Gayet, 1983, p. 189). In *L. niloticus* this bone is reported to be rather flat in lateral view and the foramen for the hyomandibular nerve directed almost completely to the lateral side. *L. maliensis* has a more convex prootic with the foramen facing posteriorly. Moreover, the lateral commissure is wider in *L. maliensis* than in *L. niloticus*.

In our sample of recent *L. niloticus* skeletons from the Niger and the Nile, a wide variation is observed for the degree of flatness of the prootic and the width of the lateral commmissure. However, it is difficult to quantify these criteria. The direction of the foramen for the hyomandibular nerve is not constant either; in the majority of our *L. niloticus* specimens the foramen is facing posteriorly as in *L. maliensis*.

EXOCCIPITAL

Contrary to the condition in *L. niloticus*, the foramen for the vagus nerve is described as being situated at the end of a deep groove ("au fond d'une profonde gouttière") in *L. maliensis* (Gayet, 1983, p. 189). This feature is again highly variable in our recent *L. niloticus* specimens, but it seems that the formation of a groove is age related (Table IV). In the description of the *L. maliensis* material only one exoccipital is mentioned of an individual between 60 and 70 cm long (Gayet, *ibid.*, p. 186), a length at which recent *L. niloticus* a groove may already have formed.

POSTERIOR PART OF THE NEUROCRANIUM

According to Gayet (1983, p. 189) the skull of *L. maliensis* widens more than in *L. niloticus* at the level of the parietal crests. As a result of this the epioccipitals are separated from the supraoccipital crest by a greater distance in *L. maliensis*. Moreover, the epioccipitals are sturdier than in *L. niloticus* and their posterior processes extend further.

The sturdiness of the epioccipitals and the degree of posterior prolongation are extremely variable in our sample of recent *L. niloticus*, and are apparently not correlated with age. In specimens of about the same skull length (nr. 267 and 240), one individual has long posterior processes, whereas in the other very sturdy epioccipitals are observed. Even within one individual the epioccipitals may be unevenly developed, as in specimen nr. 276 where one of them is sturdy and the other one slender.

The reported posterior widening of the neurocranium has been investigated as well, but it was hard to find reproducable measurements that can quantify the degree of enlargement. We found only a restricted variability in the posterior widening, but *L. niloticus* specimens comparable to the *L. maliensis* figured by Gayet (*ibid.*, Pl. XIX-1) are present in our collection.

PREOPERCULUM

The preoperculum of *L. maliensis* is reported to differ from that of *L. niloticus* in the degree to which the lateral line canal is open. In *L. niloticus* the canal is almost completely bone enclosed, with only a few pores in the horizontal branch, whereas in *L. maliensis* the horizontal part of the canal is more open. In a large specimen (more than 90 cm) of *L. maliensis* the preopercular canal was open from the anterior part of the bone to the level of the second spine. In a smaller individual of approximately 50 cm, the lateral line canal was closed only by two narrow bone bridges (Gayet, 1983, p. 189).

In our recent *L. niloticus* specimens, the presence and degree of development of the first two anteriorly situated bony bridges were verified (see Fig. 3). The first bony bridge was always present in the Nile specimens, but this was not the case of the Niger fish. The bridge was absent in four specimens, not completely bridging the sensory canal in seven and it was normally developed in nine. The second bony bridge was seen in all the Niger and Nile specimens, but the width seemed to be variable. We gained the impression that on average the bony bridge was wider in the Nile specimens.

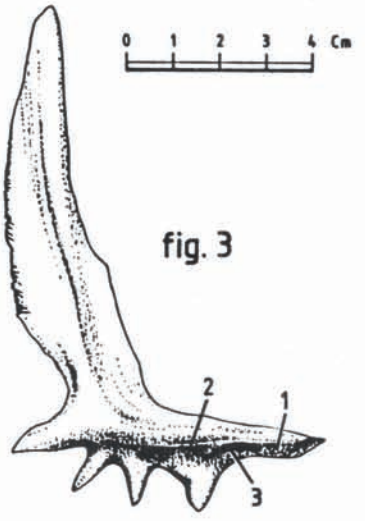
According to Gayet (*ibid.*) the first spine of the preoperculum is heavier in *L. maliensis* than in *L. niloticus*. We found that there is an important variability in the size and shape of the first (and other) spines, even within one individual. Heavy spines such as figured for *L. maliensis* (Gayet, ibid., Pl. XVI-2; Pl. XIX-11) were also found in our recent *L. niloticus*.

OTOLITH

Two saccular otoliths of *L. maliensis* occur in the inventory of the material given by Gayet (1983). The figured specimen (Gayet, *ibid.*, Pl. XVIII-7), has been examined by Dr Nolf (Brussels), who compared it to *L. calcarifer* and the extant species living in Lake Tanganyika. He concluded that the fossil otolith does not correspond to any of these species. It should be underlined, however, that *L. niloticus* does not occur in Lake Tanganyika at the present-day. The few otoliths that we have in our *L. niloticus* collection correspond well in shape to the *L. maliensis* specimen figured by Gayet (*ibid.*).

DENTARY

L. maliensis and *L. niloticus* are said to differ in that the dentary of the former species is more slender. The ratio of the length of the dentary (taken from the symphysis to the upper pore of the mandibular canal) to its height, taken at the level of the pore, would equal approximately 2.5 in *L. maliensis* and only 1.5 in *L. niloticus* (Gayet, 1983, p. 189). The measurements taken on our recent



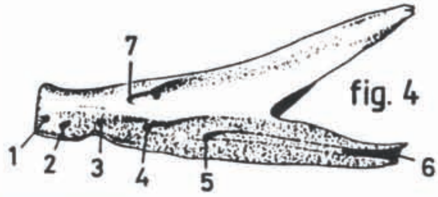


Fig. 3 : Lateral view of right preoperculum of recent *L. niloticus* (specimen nr. 275). 1 and 2: bony bridges; 3: sensory canal.

Fig. 4 : Lateroventral view of the right dentary of *L. niloticus* (specimen nr. 267). 1 and 7: nerve foramina; 2-5: sensory canal openings; 6: posterior opening to the mandibular canal (oval pore).

L. niloticus specimens and the derived ratios are indicated in Table V. Remarkably enough all our specimens fall within the variation of *L. maliensis* and not a single one approximates the slender appearance Gayet (*ibid.*) described for *L. niloticus.*

Two further distinguishing features are related to the position of the pores to the laterosensory canal. Some confusion seems to exist, however, with respect to the nomenclature of the pores and their number (Fig. 4). Gayet (*ibid.*, p. 191 and Fig. 37) mentions four large pores to the laterosensory canal, but the anterodorsally situated pore, is not indicated by Greenwood and Howes (1975, Fig. 13B) as belonging to the group of pores to the laterosensory canal. In fact, this pore is not a mandibular sensory canal opening, but a nerve foramen (possibly the mandibular branch of the VII nerve). The lateral view of the dentary figured by Greenwood and Howes (*ibid.*) does not show any other, more posteriorly situated pores. In lateroventral view as figured by Gayet (*ibid.*), however, more pores are visible in our specimens. Gayet (*ibid.*) indicates that four large pores, including the anterodorsal one, are present in the anterior part of the dentary. If we count the pores in the same way as Gayet (*ibid.*) for the left and right dentaries we find four pores in four

Table V. Length and height measurements taken on the left dentaries of recent *L. niloticus*.

	Nr	SL (cm)	K (mm)	L (mm)	K/L
Niger	286	27	9.3	3.3	2.82
	278	31	9.9	3.9	2.54
	227	33	10.3	4.1	2.51
	302	35	11.6	4.3	2.70
	301	36	11.4	4.4	2.59
	312	38	11.9	4.8	2.48
	267	70	22.4	10.1	2.22
	240	75	22.9	8.9	2.57
	275	79	27.2	11.4	2.39
	276	80	27.9	11.9	2.34
Nile	24	13	4.5	1.6	2.81
	22	18	7.0	2.3	3.04
	67	± 20	-	-	-
	20	26	10.4	3.6	2.89
	81	30	10.1	4.0	2.53
	1	46	17.0	6.5	2.62
	57	52	19.2	7.4	2.59
	140	110	41.3	16.0	2.58

specimens, five pores in twenty-seven dentaries and six pores in three other specimens. The fifth pore that we observed most frequently is not mentioned nor figured by Gayet (*ibid.*). This discrepancy does not, however, hamper a further examination of the distinguishing features. In *L. niloticus* the fourth pore is situated posteriorly to a vertical extending from the upper pore of the mandibular canal, whereas in *L. maliensis* it lies ahead of or just on this line (Gayet, *ibid.*).

We checked the dentaries of our recent *L. niloticus* specimens, and found that in twenty-three examples the fourth pore was situated behind the vertical extending from the superior pore. Eleven specimens were comparable to *L. maliensis* : in ten the fourth lower pore lays just underneath the superior one, and in the other the fourth pore lays in front of the superior one.

A final distinguishing feature between the two *Lates* species is the size of the posterior opening to the mandibular canal. In *L. niloticus* an oval pore is situated at the posterior end of the dentary, but in *L. maliensis* this pore lays about half way along the horizontal ramus, leaving the laterosensory canal open over about half of its length. All the recent *L. niloticus* dentaries that we have seen have the oval pore situated at the posterior part of the bone.

ANGULOARTICULAR

The laterosensory canal groove should be longer in *L. maliensis* than in *L. niloticus* (Gayet, 1983, p. 191). Among the recent *L. niloticus* specimens at our disposal an important variability in the length of the groove was observed, even within one individual. Specimen 276, for instance, compares with its left side to *L. maliensis* and with its right to *L. niloticus* figured by Gayet (*ibid.*, Figs 3 and 40).

Table VI : Number of serrae observed on the left and right cleithrum of recent *L. niloticus*.

	Nr	SL (cm)	left	right
Niger	286	27	5	5
	278	31	4	4
	227	33	5	6
	302	35	6	8
	301	36	7	7
	312	38	7	9
	267	70	6	6
	240	75	8	8
	275	79	6	5
	276	80	8	11
Nile	24	13	5	4
	22	18	6	4
	67	± 20	5	5
	20	26	6	-
	81	30	5	5
	1	46	6	5
	57	52	7	6
	140	110	-	-

PREMAXILLA

According to Gayet (1983, p. 191), the space between the articular process and the posterior maxillary process is different in *L. niloticus* and *L. maliensis*. Due to a more substantial posterior maxillary process, the distance to the articular process is smaller in *L. maliensis*.

An important variability was observed in our sample of recent *L. niloticus* in the size and shape of the posterior maxillary process. Even within one individual left and right processes can be differently developed (nr. 275 and to a lesser extent 276). A limited space between articular process and posterior maxillary process, as figured by Gayet (*ibid*., Pl. XIX-3) was, however, not seen in any of our recent *L. niloticus* specimens. It was approximated by one individual only (nr. 302; 35 cm SL). For the sake of completeness it must be mentioned that none of our recent premaxillars reaches the size of the figured *L. maliensis* specimen.

QUADRATE

When viewed anteriorly the quadrate of *L. maliensis* is very similar to *L. rachirhinchus* described by Greenwood and Howes (1975, Fig. 15) in that the articulatory head and the adjacent anteroventral limb of the bone slope ventromedially at an appreciable angle (Gayet, 1983, p. 191). In *L. niloticus* it is said to be horizontal (Gayet, *ibid*.; Greenwood and Howes, *ibid*, p. 89). The majority of our recent *L. niloticus* specimens correspond to the descriptions of those authors, except in two cases. The quadrates of skeleton nr. 301 (36 sm SL) are similar to the *L. rachirhinchus* type, and an intermediate type was observed in skeleton 278 (31 cm standard length). During the examination of the quadrates it was noticed that the angle at which the element is viewed can significantly influence the attribution to one type or another.

Table VII : Width and height of the first vertebral centrum of recent *L. niloticus*

	Nr	SL (cm)	M (mm)	N (mm)
Niger	286	27	5.5	5.4
	278	31	6.4	6.4
	227	33	7.4	6.8
	302	35	7.3	6.7
	301	36	7.9	7.2
	312	38	9.0	7.6
	267	70	17.1	13.5
	240	75	17.4	14.0
	275	79	19.6	15.2
	276	80	19.8	16.0
Nile	24	13	2.4	2.3
	22	18	3.4	3.2
	67	± 20	3.6	3.1
	20	26	6.0	5.4
	81	30	6.9	5.8
	1	46	10.5	9.8
	57	52	13.1	10.0
	140	110	29.8	24.0

CLEITHRUM

According to Gayet (1983, p. 191), the difference between the cleithra of *L. maliensis* and *L. niloticus* lies in the number of serrations along the posterior border of the bone. The number of serrae would have been difficult to verify exactly in *L. maliensis*, but it seemed that there were less than 5 of them.

In *L. niloticus* more, but less developed serrations are reported to be present. Greenwood (1976, p. 40) found that the number of, sometimes ill-defined, serrae varied from 6 to 10 in *L. niloticus*. He also mentions that the number of serrae may differ on either side of an individual and that the number is obviously not correlated with the size of the serrae. Ill-defined serrations often occur in our sample and, moreover, some of the heavier serrae were slightly bifurcated. Such serrae were counted as one item only. In Table VI the number of serrae observed on the cleithra of recent *L. niloticus* is summarized, and it seems that the variation is even more important than mentioned by Greenwood (*ibid.*). As far as the size of the serrae is concerned, it must be stressed that we did not observe a cleithrum comparable to the one of *L. niloticus* depicted by Gayet (*ibid.*, Fig. 42). Moreover the figured cleithra of *L. maliensis* (Gayet, *ibid.*, Pl. XVII-6 and Pl. XVIII-1) correspond perfectly to several of our recent *L. niloticus* specimens.

FIRST VERTEBRA

The difference between the first vertebrae of *L. niloticus* and *L. maliensis* are described as follows by Gayet (1983, p. 193). A lateral depression is observed behind the exoccipital facets of *L. niloticus*, but it can be more or less filled with trabeculae, sometimes even unilateraly. In *L. maliensis* a deep, well defined fossa without any trabeculae is found, but two fossae can occur as well. In that case an extra small depression is seen above the large fossa. The small fossa may contain trabeculae, particularly in specimens of larger size.

Consultation of our recent *L. niloticus* skeletons indicates important variability in the appearance of the lateral face of the first vertebral centrum. In only one specimen a large fossa without trabeculae as in *L. maliensis* was found (at the right side of the centrum of specimen 267). All the other centra have trabeculae, but their number and the pattern in which they are organized is highly variable and results occasionally in the formation of an extra fossa. In one specimen (left side of *L. niloticus* nr. 140), such a second fossa was observed dorsally to the main depression, as in *L. maliensis*, but in another individual a small extra fossa occurs ventrally of the main depression (left side of specimen 57).

A second difference between the first vertebrae of the *Lates* species, would lay in the width/height ratio. In *L. maliensis* the centrum is supposedly wider than high, and higher than wide in *L. niloticus*. As can be seen from Table VII the latter statement does not hold for our recent specimens.

DISCUSSION AND CONCLUSIONS

Of the 25 criteria described by Gayet (1983) to distinguish *L. maliensis* from *L. niloticus*, only a few seem valid. Most of the features that should be typical of *L. maliensis* were also observed in our sample of recent *L. niloticus*. It thus seems that the variability of *L. niloticus* is indeed higher than Gayet (*ibid.*) was able to observe on the specimens at her disposal, a possibility that was underlined by Gayet (*ibid.*, p. 193) herself. As the sample of the Holocene *L. maliensis* remains was also very restricted it would be desirable to verify if the few typical features of the species that remain are valid. We suspect, namely, that they may be an artefact, resulting from differential preservation of bone tissue within one skeletal element. *L. maliensis* differs in its preoperculum by its lateral sensory canal that is open over a longer distance than in *L. niloticus*. We suppose that the relatively thin bony bridges over the canal have been preferentially destroyed by different taphonomic processes. The same may be true for the laterosensory canal of the dentary. The mandibular canal is open over half of its length in *L. maliensis*, whereas only an oval pore is present at the posterior margin of the dentary of *L. niloticus*. Preferential destruction of the fine trabeculae in the lateral fossa of the first vertebrae may also explain why these elements are absent in fossil *L. maliensis* and not in recent *L. niloticus*. That partial destruction of *Lates* bone does occur in archaeological assemblages along the ancient Holocene Niger system has been noticed by ourselves when examining a vomerine tooth patch (see p 415). The piece has the typical convex shape of *L. maliensis*, but its lateral edges are clearly broken off and the intact specimen must have been of the rather straight or slightly concave type characteristic of *L. niloticus*.

Only one characteristic of *L. maliensis* seems to hold, namely the limited space between the articular process and the posterior maxillary process of the premaxilla. Although considerable variability has been observed within *L. niloticus*, we found no recent specimen comparable to the large figured premaxilla of *L. maliensis*. It would be useful to verify further the variability within recent *L. niloticus* and within *L. maliensis*, when more material becomes available.

For the reasons just mentioned, *Lates maliensis* Gayet, 1983 is considered a junior synonym of *Lates niloticus* (Linnaeus, 1758). The implications for the palaeohydrography concern only the undated connection of the Niger and Senegal basin supposed on the basis of the presence of *L. maliensis*. This "species" or its ancestor would have entered West Africa by the Senegal river mouth. In order to colonize the investigated area in the Malian Sahara, *L. maliensis* had to migrate from the Senegal to the Niger basin, since the latter had no direct connection with the Atlantic Ocean. The fact that *L. maliensis* is in reality *L. niloticus* means that the finds in the Malian Sahara are an indication only of connections of this area with the Niger and tributaries such as the Tilemsi. A connection of Senegal and Niger basin is, however, indicated by other data. On the basis of similarities in their fish fauna the Senegal and Niger are brought together in one ichthyofaunal province, together with the Tchad basin (Poll, 1957, p. 54). From the species composition of the basins it is clear that they have been connected in a not too distant period. Geomorphological data described by Furon (1932) and Dars (1955, 1960) indicate that certain tributaries of the Senegal (Baoulé) may have had a temporarily reversed course towards the Niger.

Our study has further emphasized that there exist no particular osteological differences between *L. niloticus* from the Nile and the Niger, at least not for the features that we examined. Only the size of the pores to the lateral canal of the preoperculum seems to be smaller in Nile specimens. Size-related variability was found for only one character: a groove leading to the foramen for the vagus nerve of the exoccipital seems to develop as *L. niloticus* grows.

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